

THE PANORPOID COMPLEX.

PART I.—THE WING-COUPLING APPARATUS, WITH SPECIAL
REFERENCE TO THE LEPIDOPTERA.

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(Plates xxix.-xxx., and sixteen Text-figures.)

There can be little doubt that, in the original Pterygote Insects, fore- and hindwings were independent in flight, and the muscles controlling them were innervated from two separate sources, viz., the ganglia of the meso- and metathorax respectively. Coincidence of action or beat, then, between fore- and hindwings, without which flight would scarcely have become possible, must have been maintained through coordination of the two sets of nervous impulses sent out from these two ganglia.

Now, in those Orders in which the wings were more or less hairy, the development of a fringe round the border of the wing would undoubtedly increase the sense of touch in these organs; since the macrotrichia, or larger setæ of the wing, are of the type known as *sensillæ*, and were evidently developed at first as tactile organs. Hence it came about that, in the course of evolution, a further coordination was able to be established between the posterior portion of the base of the forewing and the anterior portion of the base of the hind.* Such coordination did not, at first, take the form of a definite linking-up of the two wings, but

* It should be borne in mind that the structures here to be discussed were originally present on *both* wings; e.g., frenular bristles occur at base of *forewings* of certain Mecoptera, as well as of hindwings; and a jugal lobe is present at bases of *both* wings in certain Trichoptera and in *Micropterygidae*. But it is only on the *posterior* border of the forewing and the *anterior* border of the hind that they can come into contact, and so develop into a coupling-apparatus.

consisted merely in the greater development of the sensillae of this region of the two wings, their contact acting as a guide in flight, much as the reins act in the driving of a horse, or the touch of the hand of one person in guiding another in the dark.

To these structures, whether they act merely as a *guide*, or whether they are more fully developed so as to *link* the two wings quite closely together, I propose to give the name "Wing-coupling Apparatus," which I have already used in dealing with the *Planipennia* (12).

The complete, archaic wing-coupling apparatus consists of four distinct parts, two belonging to the forewing, and two to the hind. These are:—

In the forewing

- (1) The area of contact with the hindwing or its bristles.
- (2) The bristles developed along the border of that area.

In the hindwing

- (3) The area of contact with the forewing or its bristles.
- (4) The bristles developed along the border of that area.

In the case under discussion, *i.e.*, when the two areas of contact are located at the bases of the wings, we may name the parts as follows:—

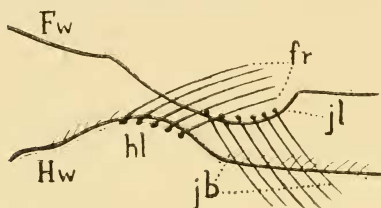
(1) The area of contact of the forewing with the hind, in so far as it projects beyond the general contour of the posterior border, may conveniently be termed the *jugal lobe*, a term I have already employed in the paper mentioned above (12). A specialised form of this area, in which it becomes an elongated, narrow process passing *below* the costa of the hindwing, is termed the *jugum*, this being the term first applied to such a process by Comstock in the *Lepidoptera* (1).

(2) The bristles projecting from this area towards the hindwing may be called the *jugal bristles*.

(3) The area of contact of the hindwing with the fore, in so far as it projects beyond the general contour of the anterior or costal border, may be termed the *humeral lobe*. I had previously employed the term *jugal process* for this area in the *Planipennia* (12). But I now consider that this term is open to objection; as

it would certainly conduce to clearness, if the adjective *jugal* were to be employed only in connection with the forewing. As authors who have written upon the Lepidoptera have generally alluded to this part of the hindwing as the *shoulder* or *humerus* (a somewhat too general term), there can be little objection in replacing it by the term here proposed.

(4) The bristles projecting from this area towards the forewing may be called the *frenulum*. This term is already in general use in the Lepidoptera, and should now be adopted for the homologous structures in other Orders.



Text-fig. 1.*

The relationships of these four parts to one another, in an ideal archaic coupling-apparatus, may be seen from Text-fig. 1, it being understood that, owing to the slightly higher level of the forewing, the frenulum passes *beneath* the jugal lobe, but the jugal bristles lie *above* the costa of the hindwing.

We may now profitably study the formation of the coupling-apparatus in the wings of the different Orders comprising the Panorpoïd Complex. From this discussion, we are compelled to omit the Protomecoptera (in which the bases of the wings have so far not been discovered in the fossils known), and the Aphaniptera, in which the wings have been lost.

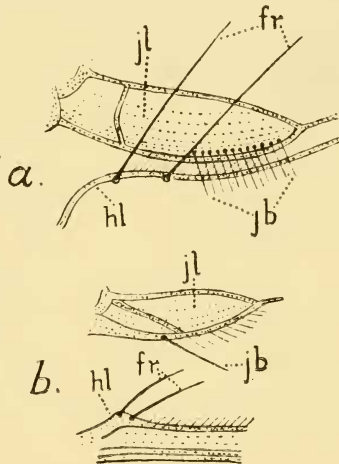
Order MECOPTERA. (Text-figs. 2-4).

This is the only Order extant in which all four parts of the ideal coupling-apparatus can still be recognised. In Text-fig. 2, I have figured the coupling-apparatus from the wings of two very archaic families, found only in Australia. In the family *Choristidae* (Text-fig. 2a), there is a slightly projecting, but quite

* Ideal archaic wing-coupling apparatus at bases of wings: *fr*, frenulum; *Fw*, forewing; *hl*, humeral lobe; *Hw*, hindwing; *jb*, jugal bristles; *jl*, jugal lobe. (Jugal bristles rest above costa of hindwing, but frenular bristles pass beneath jugal lobe of forewing).

definite, *jugal lobe* (*jl*), from the more distal portion of which arises a set of about a dozen small, but stiff and closely set, *jugal bristles* (*jb*), which make contact with the costa of the hindwing in flight. In the hindwing, there is a small but quite definite *humeral lobe* (*hl*), from which spring the two enormous bristles of the *frenulum* (*fr*). These latter, during flight, pass under—and, indeed, quite beyond the interior border of—the jugal lobe of the forewing. The whole apparatus is eminently suitable for maintaining contact between the two wings in flight, without in any way linking the hindwing *firmly* to the fore.

In the wings of the family *Nannochoristidae* (Text-fig.2*b*), which are specialised by reduction, we meet with much the same structures. But in this case there is a single, strong, jugal bristle on the forewing, instead of a set of weaker bristles. The flight of these insects is the strongest of any in the Order, and the wings are closely linked together. The linking is accomplished by the two sets of bristles. The frenulum passes *under* the jugal lobe, while the jugal bristle passes above the bases of the frenular bristles, and presses down upon the costal area of the hindwing, thus forming a very neat and perfect coupling-apparatus.



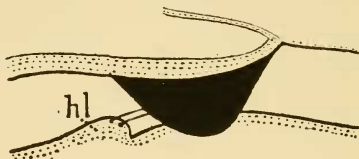
Text-fig.2.*

In the archaic *Meropidae* (Text-fig.3), there is a peculiar specialisation not found anywhere else, to my knowledge, within the Insecta. The jugal lobe bears a very distinct, black tubercle, projecting from its border. This tubercle appears to have been

* Wing-coupling apparatus in Mecoptera. a, In *Tanniochorista pallida* E.-P., wings connected, viewed from beneath. b, In *Nannochorista dipteroides* Till., wings disconnected. (Both $\times 83$). Lettering as in Text-fig.1.

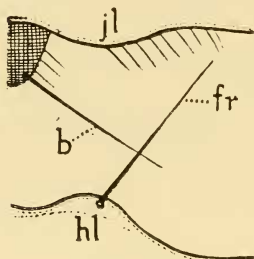
formed by fusion of an original set of jugal bristles, as seen in *Chorista*. A frenulum is also present, but reduced in size.

In all other representatives of this Order, the jugal bristles appear to be either absent or very weakly formed; and the whole coupling-apparatus shows a gradual reduction from disuse, probably owing to a progressive weakening in the flight of these somewhat lazy insects.



Text-fig. 3.*

The culmination of this tendency is to be seen in the highly specialised *Bittacidae*, in which fore- and hindwings have again returned to complete independence in flight, the wings becoming greatly narrowed and elongated, with petiolation of their bases. The coupling-apparatus is here only represented by a vestige of the humeral lobe, from which projects a single frenular bristle, which crosses a similar bristle developed from the extreme base of the forewing (Text-fig. 4).



Text-fig. 4.†

Reviewing the above evidence, it is clear that the Archetype of the Order Mecoptera must have had the complete archaic coupling-apparatus fully developed, very much as it still exists in the ancient *Choristidae* to-day.

Order PLANIPENNIA. (Text-fig. 5).

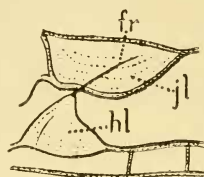
In this Order, the coupling-apparatus is again best developed in the more archaic families, notably in the *Heimerobiidae* (Text-fig. 5). Jugal bristles are absent; but the frenulum is represented either by one or two strong bristles (*fr*). These bristles

* Wing-coupling apparatus in *Merope tuber* Newm., viewed from above, showing the large, black tubercle at base of forewing; *hl*, humeral lobe; ($\times 40$).

† Reduced wing-coupling apparatus in *Harpobittacus tillyardi* E.-P : *b*, bristle developed from extreme base of forewing; other lettering as in Text-fig. 1; ($\times 40$).

project from the apex of a very strongly developed humeral lobe (*hl*). During flight, this latter lobe, together with its frenulum, passes under the jugal lobe of the forewing, which is hollowed out beneath for its reception.

The same type of coupling-apparatus is to be found in all the other families, but it is generally much reduced in size, and does not appear to be functional. The tendency in the evolution of this Order has been to combine a progressive narrowing of the wings with a gradual return to complete independence of fore- and hindwing in flight. In the highest families, *Myrmelcontidæ* and *Ascalaphidæ*, the bases of the wings become shortly petiolate, and the original coupling-apparatus can only be made out as an extremely reduced remnant at the very bases of the wings.



Text-fig. 5.*

For this Order, then, we must assume an Archetype in which the archaic coupling-apparatus was complete in all except one particular, viz., that the jugal bristles were absent.

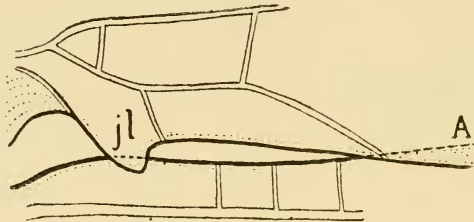
Order MEGALOPTERA. (Text-figs. 6-7).

Throughout this Order, the hairy vestiture of the wings, both macro- and microtrichia, has been very much reduced. The most archaic type of coupling-apparatus known to me within the Order is to be found in a genus not yet described, but allied both to the *Corydalidæ* and the *Sialidæ*. This possesses both jugal and humeral lobes, of small size, the latter with a few small hairs, the remnants of the frenulum. In *Sialis*, the two lobes are present, but apparently hairless.

In the *Corydalidæ* (Text-fig. 6), as exemplified by *Archichauliodes*, the only genus that I have been able to study, the humeral lobe is much reduced, but the jugal lobe becomes a definite angular projection (*jl*) which presses down upon the costa of the hindwing. Further, the forewing overlaps the hind for a con-

* Wing-coupling apparatus in *Drepanacra humilis* McL., viewed from beneath; ($\times 24$). Lettering as in Text-fig. 1.

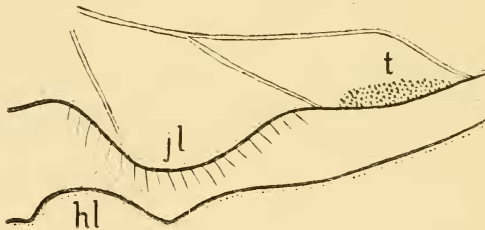
siderable distance beyond the base; and, by pressing down upon it, serves to increase the strength of the coupling in this rather powerfully-flying insect. This latter type of wing-coupling, which occurs also in many Trichoptera, and in some of the most



Text-fig. 6.

Wing-coupling apparatus in *Archichauliodes guttiferus* Walk., viewed from above; ($\times 12$). A, beginning of amplexiform overfold; jl, jugal lobe.

highly specialised Lépidoptera, I propose to term *amplexiform* (Lat. *amplexus*, an embrace). It is always correlated with the disappearance of the frenulum.



Text-fig. 7.

Reduced wing-coupling apparatus in *Raphidia maculicollis* Steph.: ($\times 40$): hl, humeral lobe; jl, jugal lobe; t, roughened tubercular patch.

In the highest family of the Order, the terrestrial *Raphidiidae*, both jugal and humeral lobes are present, but without bristles. There is, however, a very peculiar patch of roughened tubercles, situated on the posterior margin of the forewing, just beyond the jugal lobe (Text-fig. 7, t). This may possibly help in maintaining contact between the wings in flight.

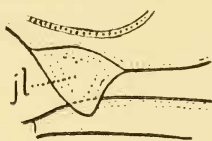
From the above evidence, we must presume that the Archetype of the Megaloptera possessed a somewhat reduced coupling-apparatus, in which the two lobes were present, the jugal bristles absent, and the frenular bristles probably quite vestigial.

Order TRICHOPTERA. (Text-figs.8-9).

In this Order, the original wing-coupling apparatus undergoes some remarkable developments, which have attracted very little notice from entomologists, so far. In all the oldest families, one can only recognise the jugal lobe, which is the *anal lobe* of systematists in this Order. This appears as a strongly projecting lobe at the base of the forewing, in such genera as *Rhyacophila* (Text-fig.8, *jl*). There are neither jugal bristles nor frenulum; and the humeral lobe is suppressed, or else only slightly developed.

In no case does this jugal lobe pass under the hindwing during flight; it merely rests upon the costa from above.

In the great majority of genera, the jugal lobe is absent or vestigial, and new elements of wing-coupling have made their appearance. This new type of wing-coupling is *amplexiform*, i.e., it is brought about by an overfold of the whole length of the anal area of the forewing upon the costa of the hind. But besides this, there are many cases in which the amplexiform coupling is strengthened by one of two new devices, as follows:—

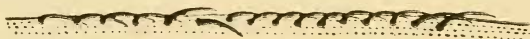


Text-fig.8.*

(1) Between the anal vein of the forewing, and the anal border, there may be developed a single row of stiff hairs, all pointing forwards and outwards, on the underside of the wing. The row of hairs upon the costal margin of the hindwing is also stiffened; so that, during flight, further strength is given to the amplexiform coupling by the intermingling of these two sets of stiff hairs. I have seen this type of coupling in an archaic Australian genus of the family *Phryganewidae*, not yet named.

* Wing-coupling apparatus in *Rhyacophila dorsalis* Pict., viewed from above; ($\times 12$): *jl*, jugal lobe.

(2) Much more commonly, and especially noticeable in the families *Leptoceridae* and *Sericostomatidae*, is a type of coupling which I propose to term *multihamulate* (Text-fig.9). In this, the row of hairs along the costa of the hindwing becomes specialised, for a greater or less length, by the development of the hairs into stiff *hooks*, which grapple the anal margin of the forewing, and so bring about a very perfect form of wing-coupling. This type will be recognised as that which also occurs universally throughout the Order Hymenoptera.



Text-fig.9.

Row of hooklets developed along the middle portion of the costal margin of the hindwing in *Oecetis* sp., (Australia); ($\times 83$).

There are many genera in this Order in which certain of the macrotrichia become developed into series of large, stiff bristles, closely resembling those of a typical frenulum. These most frequently occur along the main veins, or portions of them. Bearing this in mind, I have searched very carefully for a true frenulum in this Order, but I have not succeeded in finding one. In the males of the remarkable and highly specialised genus *Plectrotarsus*, whose systematic position within the Suborder Inæquipalpia is still a matter of dispute, I have found a set of two or three strong bristles in the position of the frenulum. But they are absent in the female, and they play no part in the coupling of the wings, which is of an advanced amplexiform type, with the jugal lobe quite small and non-functional. In two other very spiny genera, viz., *Chimarra*, and an unnamed Australian genus having whorls of numerous spines upon the tibiae, there are also stiff bristles in the position of the frenulum, at least in the males. Those of the former genus are long and slender, and are arranged in two or more irregular rows, quite unlike a true frenulum; while those of the latter are also very long and slender, irregularly placed, and lying flat along the wing, parallel to the costa. In neither case do they play any part in wing-coupling.

These developments must be regarded as isolated specialisations, which must be expected to occur throughout an Order in which all parts of the wing remain so well provided with hairs as in the Trichoptera.

From the above evidence, we must conclude that the Archetype of the Trichoptera already possessed a highly reduced coupling-apparatus, in which only one of the four original parts was represented, viz., the *jugal lobe*. This type may be designated as the *archaic jugate type* of wing-coupling.

Order DIPTERA.

In this Order, owing to the loss of the hindwings, there is no longer any need for a coupling-apparatus. But we can recognise the jugal lobe of the forewing, in the form of the basal lobe known as the *alula* in this Order.

It is clear, therefore, that the Archetype of the Diptera resembled that of the Trichoptera in possessing the *archaic jugate type* of wing-coupling, in which only the jugal lobe is present.

We might note here, parenthetically, that, in the other Holo-metabolous Order (the Coleoptera), in which flight is carried on by only one pair of wings, there may still be found evidences of the original presence of a jugal lobe; e.g., in certain *Hydrophilidæ*, where this lobe is quite large and conspicuous, though it does not seem to perform any definite function.

Order LEPIDOPTERA.

(Text-figs.10-16, and Plates xxix.-xxx., figs.1-8).

We have kept this Order to the last, because, within it, there are developed the most surprising and interesting of all the specialisations arising from the old type of basal coupling-apparatus, which we have already studied in the other Orders of the Complex.

It has been frequently stated that certain families of Moths, viz., the *Micropterygidae* (*sens. lat.*, including the *Eriocraniidae*) and the *Hepialidae*, are distinguished from all other Lepidoptera by the nature of their wing-coupling apparatus. To these, Meyrick(9) has lately added a third family, the *Prototheoridae*, which

he claims to be intermediate between the other two. These families together form the Suborder Jugatæ* of Comstock, or the group Micropterygina of Meyrick. The latter author (3, p.797) thus defines the character of the wing-coupling apparatus in this group:—"Forewings with an oblique membranous dorsal process (jugum) near base, forming with the dorsal margin a notch or sinus, which receives the costa of the hindwings. Hindwings without frenulum."

This may be taken as a standard definition of the *jugate type* of wing-coupling; provided that we add what is perhaps not quite apparent at first sight, that this true jugum passes *under* the costa of the hindwing, and so forms the notch or sinus above-mentioned, in which the costa is held as in a finger-and-thumb grip. The nature of this coupling-apparatus is best understood by referring to Text-fig.11.

As contrasted with this *jugate type*, the rest of the Order is usually regarded as forming a single Suborder Frenatæ,* in which the majority of the families possess a frenulum, but no jugum. A good definition of this character has been given by Meyrick (3, p.4):—"Generally from or near the base of the costa of the hindwing rises a stiff bristle or group of bristly hairs, termed the *frenulum*, of which the apex passes under a chitinous catch on the lower surface of the forewing, termed the *retinaculum*, thus serving to lock the wings together; the frenulum is commonly single and strong in the male, multiple and weak in the female; the retinaculum in the female is commonly represented by a group of stiff scales."

However, certain families of the Frenata, including the great division Rhopalocera or Butterflies, do not possess this frenulum. In these forms, the coupling of the wings in flight is brought about by the downward pressure of the posterior margin or dorsum of the forewing upon the costa of the hind, the latter, on its part, pressing strongly upwards from beneath. The humeral

* I fail to understand the use of the *feminine* plural, since these words are adjectives, and should agree with the neuter plural noun *Lepidoptera*. I propose, therefore, in future, to write them *Jugata* and *Frenata*, respectively.

lobe of the hindwing is generally fairly large in these forms, thus allowing a greater area of the hindwing to pass under the fore than would be the case if it were normal in size. Thus it will be seen that the type of coupling here represented is that which I have already termed, in the Megaloptera and Trichoptera, *amplexiform*. I propose to use this term to distinguish these groups from those possessing a frenulum, without in any way thereby indicating a belief that the amplexiform groups in the Lepidoptera constitute a single line of descent. For it must be evident that there is no reason why the frenulum may not have been lost independently along several distinct lines of descent, leaving us at the present time with several isolated amplexiform groups, each of which has its nearest relationship, not with the other *Amplexiformia*, but with a different frenate group.

As an illustration of this, we find, in the *Castniidae*, a family in which both the frenulum and the humeral lobe are well developed. From such a group, either a typical Frenate group or a typical Amplexiform group might be descended; the former by reduction of the humeral lobe, the latter by loss of the frenulum.

Considering that the condition of the wing-venation is of greater importance than the structure of the wing-coupling apparatus, for the purposes of classification, I have already, in a preliminary report on this research(13), suggested that the primary division of the Lepidoptera into two Suborders should be based upon the former instead of the latter. I therefore defined two Suborders as follows:—

i. Suborder HOMONEURA.

Venation of fore- and hindwings closely similar and of primitive design. (Families *Micropterygidae* (*sens. lat.*), *Prototheoridae*, and *Hepialidae*).

ii. Suborder HETERONEURA.

Venation of hindwing reduced, and differing widely from that of the forewing. (All the other families).

The reason for discarding the older terms *Jugata* and *Frenata*,

in favour of this new division, will be more fully appreciated when we have completed our study of the *Micropterygidae*.

Adopting, then, the above terminology, we may now proceed to study in more detail the type of wing-coupling apparatus to be found in the two divisions or Suborders.

i. Suborder HOMONEURA.

Family MICROPTERYGIDÆ (*sens. lat.*).

(Plate xxix., figs.1-4, and Text-fig.10).

In this family, I made preparations from the wings of all five genera available to me, viz., *Sabatinca*, *Micropteryx*, *Mnemonicæ*, *Eriocrania*, and *Mnesarchææ*.

I should like here to thank the many kind correspondents who have supplied me with specimens of this family, at all times difficult to obtain; and, in particular, Mr. Meyrick, for a series of set specimens representing all five genera; Mr. A. Philpott, for various New Zealand species, both set and in spirit, and for his valuable observations on the flight of *Sabatinca*; and Mr. K. J. Morton, of Edinburgh, for a large number of spirit-specimens, which yielded excellent mounts and dissections.

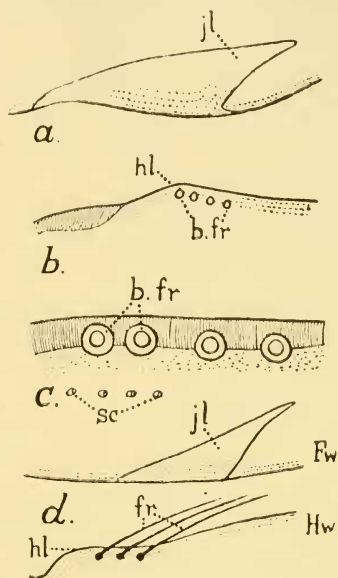
In dealing with this family, I was at once struck by the behaviour of the so-called *jugum* in cleared and mounted specimens. Instead of arranging itself as a free lobe at the base of the dorsum of the forewing, I found that it always insisted upon remaining twisted under the wing itself, and that this position could only be altered with difficulty, by drawing the *jugum* out from under the wing with a needle. (Plate xxix., fig.1, and Text-fig.10*a*, *d*).

Referring to figures of this *jugum* already published, I found that Comstock(1), Forbes(8), and Meyrick(3, 4) had all figured it as a projecting lobe, whereas Packard(10, 11) alone had depicted the true position; though without, apparently, any idea of its significance.

Turning next to the examination of cleared and descaled mounts of the hindwing, I found invariably from three to six large bases of insertion (Plate xxix., fig.3, and Text-fig.10, *b*, *f*, *r*.)

of a circular shape, situated along the costal border in the region of the humeral lobe, this latter being only a slight prominence. Comparing these with the bases of insertion of neighbouring scales (*sc*), I found that they were of very much greater size, as well as of more regular shape. It was evident, therefore, that they were not the bases of either typical scales or of hairs, but that they must belong to a series of strong *bristles*, which had been removed during the process of descaling. This led me to infer the presence of a true *frenulum* in this family.

The next step was to examine set specimens from the underside, under a fairly high power of the microscope. To do this, I clipped off the pin close to the underside of the thorax, and then inserted the head of the pin into a piece of indiarubber, so that the moth was exposed ventral side uppermost. By this means the lens could be brought close down upon the wings, without touching the pin.



Text-fig. 10.*

The immediate result of this examination was the discovery of a set of strong bristles, nearly always three or four in number, more rarely two, five, or six, constituting a *true frenulum*, but directed outwards and upwards at a very slight inclination to

* Wing-coupling apparatus in *Sabatinca incongruella* Walk., (New Zealand, fam. *Micropterygidae*): *a*, base of dorsum of forewing in ♀, viewed from beneath; ($\times 83$): *b*, base of costa of hindwing in ♀ (descaled); ($\times 83$): *c*, portion of the same enlarged, to show insertions of frenular bristles (*b.fr.*) and insertions of scales (*sc.*) from a part of the same wing for comparison; ($\times 320$): *d*, bases of wings in ♂, the forewing viewed from beneath, the hindwing from above; ($\times 83$): *fr.*, frenulum; *hl*, humeral lobe; *jl*, jugal lobe. (Cf. Plate xxix., figs. 1-4).

the costa of the wing (Text-fig.10, *fr*). *It is these bristles, and not the costa of the hindwing itself, which become engaged in the slit or sinus formed between the jugum and dorsum of the forewing.* Although the difficulty of setting these tiny moths in the natural position must be very great, I actually found three specimens in which one or both wings had become engaged in the natural manner; and one of these came from Mr. Meyrick's own collection.

Wishing to have my result tested in the field, I wrote at once to Mr. A. Philpott, of Invercargill, N.Z., asking him to investigate the coupling-apparatus in the wings of the living insect, and sending him careful drawings of my results. The only species that he was able to study was a new species of *Sabatinca*, of which he reported that the coupling apparatus was exactly the same, in structure and position, as that of *S. incongruella*, represented in my drawings. He also added some valuable notes on the habits of flight and rest in this species.*

We come, then, to the following conclusions with regard to the *Micropterygidae*:—

(1) In so far as it is a fact, that a definite and well-developed frenulum is present in this family, they are of a *frenate* rather than a *jugate* type.

(2) In so far as the so-called jugum does not pass backwards under the hindwing, so as to engage the costa in a finger-and-thumb grip, it is not a true jugum, but must be termed a *jugal lobe*; also, for the same reason, these moths are not true *jugate* types.

(3) Since the jugal lobe is turned forwards under the forewing, and acts as a catch for the frenulum, it is clear that it should be regarded as an archaic form of *retinaculum*, analogous to, but not homologous with, the retinaculum found in the true Frenate forms.

(4) From this, it will be seen that the *Micropterygidae* combine in themselves certain characters belonging to both Jugate and Frenate types.

* These are given in an Appendix to this Part, on p.318.

I propose, therefore, to designate the kind of wing-coupling apparatus found in this family as *Jugo-frenate*.

Apart from the specialisation shown in the actual underfolding of the jugal lobe, and the consequent alteration in the direction of the frenular bristles, so as to lie more nearly parallel with the costa of the hindwing, it will at once be seen that this type of coupling is the exact homologue of that found in the older Orders Mecoptera and Planipennia. It agrees more closely with the latter, since both have lost the jugal bristles; but differs from it in the larger number of frenular bristles, and in the less definite development of the humeral lobe.

Thus we come to the logical conclusion, that the archaic jugo-frenate type, found in the older Orders of the Panorpoid Complex, is represented, at the very base of the Lepidoptera, by a somewhat more specialised jugo-frenate type, in which the retinacular nature of the jugal lobe, already existing in the Planipennia, is more accentuated by underfolding, so that the frenular bristles are held in a firmer grasp.

Having now fully reviewed the position in the *Micropterygidae*, we may pass on to consider the more specialised families.

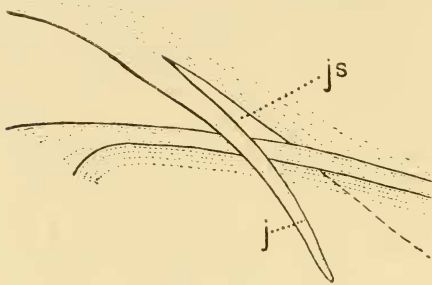
FAMILIES HEPIALIDÆ and PROTOTHEORIDÆ.

(Plate xxx., fig.5, and Text-figs.11-12).

In the *Hepialidae*, I have studied all the Australian genera available, together with the Palearctic genus *Hepialus*, of which I possess a number of specimens. In the *Prototheoridae*, through the kindness of Dr. Péringuey, Director of the South African Museum, Capetown, I have received two specimens for study, one of which proved to belong to Mr. Meyrick's *Prototheora petrosema* (9), while the other appears to represent a new species, not yet described.

The typical *jugum* found in the great majority of the *Hepialidae*, and also in the genus *Prototheora*, is shown in Text-fig.11, and also in Plate xxx., fig.5. It is a long and fairly stiff finger-like process (in most species carrying very long and abundant hairs), which projects well below the costa of the hindwing during flight, and engages it in a strong finger-and-thumb grip.

The resulting flight is, in most cases, exceedingly swift and strong; indeed, there is one Australian species common enough about Sydney, *Perissectis australasiae* Don., in which the males



Text-fig. 11.*

fly so swiftly as to be almost invisible, and are most difficult to catch. One has only to watch, too, the manœuvres which both sexes carry out during courting, to be convinced that dexterity of flight is carried very far in this family, and is certainly not surpassed by the greater number of Heteroneurous forms. We may, therefore, regard this true jugate type as a high specialisation, very superior to the jugo-frenate type of the *Micropterygidae*.

In the genus *Prototheora*, I find no difference from the typical jugate type of the *Hepialidae*. The jugum is long and narrow, and the costa of the hindwing is quite devoid of bristles.

In the new (undescribed) species of the *Prototheoridae* which I examined, there is a more primitive type of jugum, in the form of a triangular lobe, only slightly more prominent than that to be seen in many Trichoptera. As in this latter Order, this lobe does not act as a true jugum, but appears to rest upon the upper surface of the hindwing, just overlapping the costa. I do not know whether this character is a constant for this species, having only examined one specimen. It should be noted that, in studying a long series of *Hepialidae*, a very similar development manifests itself occasionally in one or both wings, especially in the genera *Charagia* and *Porina*. Such occasional developments are to be regarded as strictly atavistic, and indicate the evolution of the highly specialised *jugum* from the older *jugal lobe*.

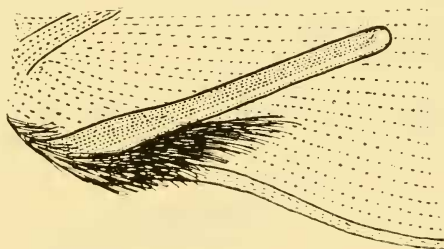
* Wing-coupling apparatus in *Charagia eximia* Scott, viewed from beneath, with hairs removed; ($\times 12$): *j*, jugum; *js*, jugal sinus. (Cf. Plate xxx., fig. 5).

Some interesting deviations from the normal jugate type may now be noted in the *Hepialide*:—

(1) In the genus *Pielus*, the jugum is a hard chitinous rod, somewhat truncated at its tip, and placed so as to project definitely beneath the anal area of the forewing (Text-fig.12). It is quite impossible to make this rod pass under the costa of the hindwing, either in the living or freshly-killed insect. But it will fit quite easily *above* the costa of the hindwing, near the base, where there can be found, in specimens that have been on the wing, a deep groove worn in an oblique direction in the dense hairs that clothe the area around the humeral cross-vein.

It would appear, then, that this genus differs from the rest of the family in having the jugum resting *above* the costa, not beneath it, and also in the structure and position of the organ itself. We should, therefore, regard this genus as highly specialised.

(2) In the genus *Leto*, some specimens show a very weakly formed jugum of very small size for the bulk of the insect: while others have none at all. The bases of the wings are densely clothed with long, soft hairs. The method of coupling in these magnificent insects, which are said to have great



Text-fig.12.*

powers of flight, appears to be practically *amplexiform*, the anal field of the forewing being bounded anteriorly by a very strongly developed 1A, and overlapping the costa of the hindwing to a considerable extent in flight.

(3) In the small moths of the genus *Fraus*, the jugum is very short, yet it undoubtedly secures the costa of the hindwing in

* Jugum of *Pielus hyalinatus* Don., ♀, viewed from beneath, to show natural position under anal area of forewing; ($\times 6$).

the typical manner. Of the New Zealand *Porina umbraculata*, Mr. Philpott writes, "the jugum is so small as to seem worthless as a coupling in the manner of finger-and-thumb."

Thus we see that there is a considerable diversity in the form and function of the jugum, as developed in the *Hepialidae*.

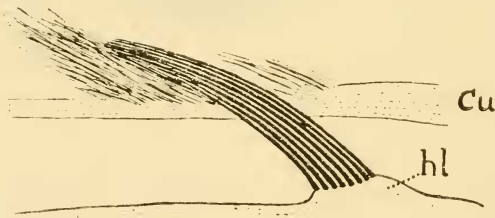
The discussion as to how the highly specialised jugum of the *Hepialidae* is related to the jugo-frenate type of coupling-apparatus found in the *Micropterygidae* is best left until we have dealt with the Heteroneura.

ii. Suborder HETERONEURA.

A. FRENATE TYPES. (Plate xxx., figs.6-8, and Text-figs.13-16).

Meyrick's excellent definition of the frenate type has already been quoted on p.296. We may now profitably study, in more detail, the differences between the female and male types.

These differences are clearly correlated with differences in the power and frequency of flight. In those forms in which the female flies but little, the frenulum remains small, and composed of a number of separate bristles, while that of the strongly-flying male may be very large and strong. But in other forms, in which both sexes fly almost equally well, the frenulum of the female may be almost as strongly formed as that of the male, though never consisting actually of a single bristle.



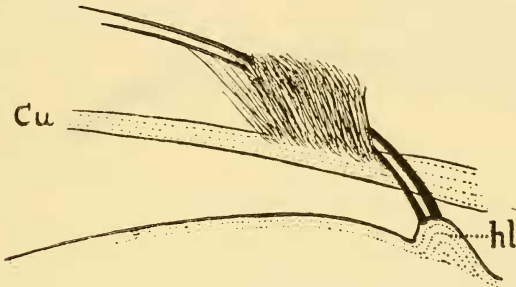
Text-fig. 13.

Wing-coupling apparatus of *Hippotion scrofa* (Boisd.), ♀, showing frenulum of eight separate bristles, and retinaculum of hairs arising from cubitus (*Cu*): viewed from beneath; ($\times 16$): *hl*, humeral lobe.

Text-fig. 13 shows the *frenulum* of a female Sphingid (*Hippotion scrofa* Boisd.). The bristles composing it are eight or nine in

number, all quite separate, but closely set together, as shown in the figure.

The *retinaculum*, or catch, which holds these bristles in place, is a very generalised structure, being nothing more than the somewhat stiffened hairs or scales which arise from the underside of the cubital vein of the forewing, and run obliquely forward and distad. The manner in which the frenulum is held in place by these hairs is closely similar to that by which the jugum of *Picus* is held in its groove by the hairs on the costa of the hindwing.



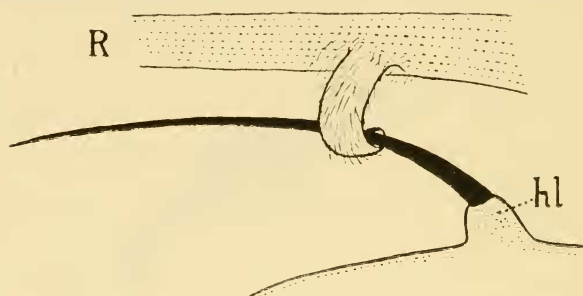
Text-fig. 14.

Wing-coupling apparatus of *Plusia verticillata* (Guér.), ♀, showing frenulum of two strong bristles, and retinaculum of stiff hairs arising from cubitus (*Cu*); viewed from beneath; ($\times 30$): *hl*, humeral lobe.

In the Noctuid genus *Plusia*, in which males and females fly almost equally well, we may see a much more highly specialised coupling-apparatus in the female. Here, the frenulum is composed of only two (sometimes three) bristles, apparently formed by the fusion of an original greater number, and almost as long as those of the male. The retinaculum, too, is more strongly developed, the hairs being stiffer and more closely set, so as to form a very definite catch for the frenulum (Text-fig. 14).

Turning next to the males, we find, in every case, a highly specialised condition present (Plate xxx., fig. 8, and Text-fig. 15). Here, the frenulum is represented by a single huge bristle, which may even reach to more than half the length of the wing, as in the family *Psychidae*. As Packard (10) has already shown,

if this apparently single bristle be cut across near its base, the separate interior channels of the bristles of which it is actually composed can be easily recognised. Thus, we see that the large, male frenular bristle is not formed by hypertrophy of one of the original series at the expense of all the rest, but by fusion and lengthening of the whole set. The longitudinal fluting visible along the somewhat flattened basal part of this bristle is also evidence of its composite nature.



Text-fig. 15.

Wing-coupling apparatus of *Hippotion scrofa* (Boisd.), ♂, showing single, strong, frenular bristle, engaged in hasp-like chitinous retinaculum developed from the radius (*R*); viewed from beneath; ($\times 14$); *hl*, humeral lobe.

The *retinaculum* in the male is a highly specialised structure, having no homologue in the female, or in any other insect. It consists of a strong, curved, chitinous catch, directed posteriorly towards the hindwing, and developed from the underside of the strong radius of the forewing, not very far from its base. This structure is hasp-shaped, and forms a very efficient catch for the frenulum, which is able to slide to and fro within its grasp, during flight, without running any risk of becoming detached (Text-fig. 15).

It is curious to note the difference in action required for the coupling of the wings in the two sexes, owing to the difference in position of the retinaculum. In the female, we must move the *hindwing* sharply forward, and then let it fall gently back, so that the frenulum may become engaged in the catching hairs.

But it is necessary to move the *forewing* sharply forward, if one desires to secure the coupling of the two wings in the male. In doing this, the stationary frenulum is caught up by the moving hasp-like retinaculum; and the grip, once effected, is not easily lost.

We may summarise these results briefly as follows:—

Female.—Unspecialised *frenulum* of from two to nine separate bristles set closely together. Unspecialised *retinaculum* of stiff hairs or scales directed anteriorly, and developed from the underside of the cubitus of the forewing.

Male.—Specialised *frenulum* of a single, large, composite bristle, formed by fusion of the original series of separate bristles. Specialised *retinaculum* in the form of a chitinous hasp, directed posteriorly, and developed from the underside of the radius.

B. AMPLEXIFORM TYPES.

The groups which have lost the frenulum and adopted the *amplexiform* type of wing-coupling (in which connection is maintained simply by overlapping of the anal area of the forewing upon the well developed costal area of the hind, including the enlarged humeral lobe) may be arranged in three super-families; viz., the Saturniina, the Lasiocampina, and the Papilionina or Rhopalocera. These three do not appear to be very closely related.

The Saturniina comprise the large and highly specialised group of the Atlas Moths or Emperors. These possess neither frenulum nor proboscis, and have a highly specialised venation. Meyrick places them as the last of his series Notodontina; but this arrangement does not seem to be generally accepted by other Lepidopterists.

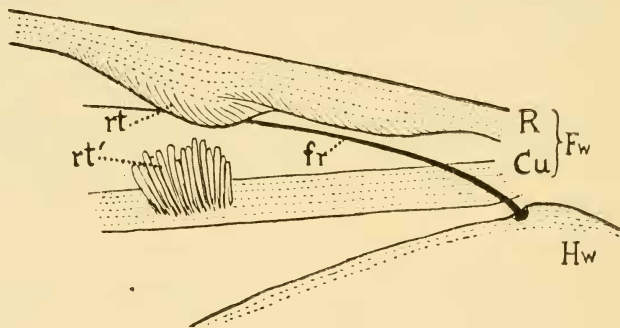
The Lasiocampina form a natural group, if the *Eupterotidae* and *Drepanidae* be included in them. In the former family, a frenulum is present; in the latter, most of the genera show a small or reduced frenulum. In the other two families, the *Endromidae* and *Lasiocampidae*, the frenulum is absent. These last show a very high specialisation of the amplexiform arrangement, in certain genera. For instance, in *Lasiocampa*, the

humeral lobe is greatly enlarged, and is supported by a series of recently formed ribs or cross-veins.

The Papilionina form another natural group, whose origin appears to be much in doubt. Meyrick and Hampson consider them to be derived from the *Thyrididae*. The *Hesperidae*, however, grade so closely into the *Castniidae* in Australia, where forms like *Euschemon* are of Hesperiid structure in all but the possession of the frenulum, that it is difficult to cast aside the belief, held by the opposite school of Lepidopterists, that the *Castniidae* closely approximate to the ancestral form from which the higher Butterflies, through the *Hesperidae*, have been derived.

C. THE FAMILY CASTNIDÆ.

Much light can be thrown upon the evolution of the two types of frenulum, in the male and female of Heteroneura respectively, as well as upon the origin of Amplexiform types, by the study of



Text-fig. 16.

Wing-coupling apparatus of *Syneemon hesperoides* Feld., ♂, viewed from beneath; ($\times 14$): *fr*, frenulum; *Fw*, forewing; *Hw*, hindwing; *rt*, retinaculum developed from radius (*R*); *rt'*, retinaculum developed from cubitus (*Cu*); in ♀, this latter alone occurs.

the family *Castniidae*.* In this family, both the humeral lobe and the frenular bristles may be seen well developed, in such a genus as *Syneemon* (Text-fig. 16). In the males of this genus, the

* For the supply of material for study in this family, I am indebted to Mr. Geo. Lyell, F.E.S., of Gisborne, Vic.

frenulum is of the usual type, *i.e.*, elongated, and with all the bristles fused together into a single, strong bristle. In the female, there are two long and delicate bristles (as in *Plusia*) accompanied usually by several shorter bristles at their base. The retinaculum of the female is of the usual type, consisting of a patch of forwardly projecting scales, developed on the under-side of the cubitus of the forewing; but this retinaculum is situated so far from the wing-base, that only the two longer bristles can become engaged in it, and the connection appears to be easily lost during flight. In the male, this retinaculum of scales upon the cubitus is *retained quite conspicuously* (Text-fig. 16, *rt'*), together with an additional development of a *slight overfolding* of the edge of the radius in a backward direction (*rt*). Usually, during flight, the frenulum of the male is caught in the curve of this overfold, as shown in the figure. But if, at any time, the frenulum slips out of this somewhat precarious hold, it is then caught up by the still existing retinaculum on the cubitus, and the insect can continue its flight in the manner of the female.

Thus we see that, in *Syuemon*, the type of coupling-apparatus for the wings is much closer, in the two sexes, than it is in other frenate moths; and we can scarcely doubt that the condition in the male of this genus is that which preceded, in the males of other frenate moths, the more specialised condition that we find in them at present.

If now, we turn to the genus *Euschemon*, which is claimed by some authors as a moth, by others as a butterfly, we find that the male has a well-developed frenulum and retinaculum of the type found in other frenate moths, *i.e.*, more highly specialised than in *Syuemon*. But, on examining the female, I was surprised to find no trace whatever of a frenulum or retinaculum; and it is evident that this sex couples its wings in the amplexiform manner of the Butterflies, by means of its large humeral lobe. Thus, judged only on the form of its wing-coupling apparatus, the male of *Euschemon* is a frenate moth, the female a butterfly. This genus, then, exactly bridges the gap between the old subdivisions Heterocera and Rhopalocera. That this is not a mere

chance convergence, I shall hope to prove in detail later on, when we come to consider the question of larval forms; the larva of *Euschemon* being, in almost every respect, that of a typical Hesperiid.

From the above evidence, the origin of the Amplexiform type of wing-coupling in the Butterflies is naturally suggested as follows. The ancestors of the Butterflies must have had a wing-coupling apparatus of the type seen in *Synemon* at the present day. By developing a manner of flight differing from that of the moths, principally in the greater amplitude of wing-stroke but lesser number of vibrations per second, the delicate, elongated bristles of the frenulum in the female first began to fail to hold the wings in position. The retinaculum being already too far out for the shorter bristles to be of any use, the whole frenular apparatus would then rapidly become aborted, and the insect would depend upon the pressure exerted by the large humeral lobe of the hindwing for keeping the wings in position. That is to say, the Amplexiform type of wing-coupling first became adopted in the female only, as we see it in *Euschemon* at the present day. Next, considering the question of the male, evolution could still proceed along one of two directions: either the overfolding of the radius might continue to increase, until an efficacious, hasp-shaped retinaculum (of the type seen in most male frenate moths) had been developed, thus saving the stronger frenulum of this sex from extinction; or the line of evolution might follow that of the female, presumably by the change in the method of flight making it impossible for even this strong frenulum to continue its hold upon the retinaculum, at a time when the latter had not yet reached the hasp-shaped stage. In that case, frenulum and retinaculum would, in the end, become aborted, as in the female, and we should arrive at the full Amplexiform type exhibited by the Butterflies in both sexes.

The following Table will exhibit, in a concise manner, the differences in the condition of the wing-coupling apparatus studied above:—

Group	Sex	Frenulum	Retinaculum on cubitus	Retinaculum on radius
Typical Heteroneura	♀	short unfused bristles	present	absent
	♂	single long bristle (original bristles fused)	absent	present
<i>Castniida</i> :—				
<i>Synemon</i>	♀	two long and several short bristles, unfused	present	absent
	♂	single long bristle (original bristles fused)	present	present, weakly formed
<i>Euschemon</i>	♀	absent	absent	absent
<i>Euschemon</i>	♂	single long bristle (original bristles fused)	absent	present, as a strong hasp
Papilionina	♀ ♂	absent	absent	absent
Saturniina* Lasiocampina* (<i>par-</i> <i>tim</i>)				

FORM OF THE COUPLING-APPARATUS IN THE ARCHETYPE OF THE LEPIDOPTERA.

Reviewing all the above evidence, it becomes clear that the oldest existing form of coupling-apparatus, viz., that of the *Micropterygidae*, is already specialised in a direction from which

* It is not suggested here that the evolution of the amplexiform type in the Saturniina and Lasiocampina has been along the same lines as that of the Papilionina. In the Lasiocampina, at any rate, a study of the conditions to be seen in the *Drepanidae* would suggest a direct descent from Eupterotid-like ancestors with the frenate wing-coupling apparatus fully developed. Thus the Papilionina are probably of remoter origin than either the Saturniina or the higher families of the Lasiocampina.

the true Jugate and Frenate types cannot possibly be derived, because of the alteration of the direction of the frenular bristles, and the turning-under of the jugal lobe. We must conclude, therefore, that the Archetype of the Lepidoptera possessed a primitive jugo-frenate type of coupling-apparatus, of the form found in the Planipennia; *i.e.*, with all parts present and normal, except the jugal bristles, which were absent.

GENERAL CONCLUSIONS.

Reviewing the evidence afforded by all the Orders of the Panorpoïd Complex, we may legitimately arrive at the following conclusions:—

(1) The original coupling-apparatus was situated at the bases of the wings, and was of a primitive *jugo-frenate* type, in which each wing developed a slight lobe towards the other, and these lobes bore projecting bristles which came into contact, and so set up a tactile connection between the two wings, to help in the coordination of the act of flight. By increase in the size of the lobes, or the length of the bristles, the connection became of a more intimate kind, a certain amount of pressure being exerted to keep the wings in position during flight.

In this primitive type, there were originally four elements represented, *viz.*, the *jugal lobe* with its *jugal bristles* on the fore-wing, and the *humeral lobe* with its *frenulum* on the hind.

(2) The only Order which has retained this ancient type of coupling-apparatus in its entirety is the Mecoptera; and, in this Order, the apparatus is only fully functional in the two archaic families *Choristidæ* and *Nannochoristidæ*.

(3) By loss of the jugal bristles, and by increase of the size of the two lobes, there arose the modification of the jugo-frenate type seen in the Planipennia. This also is only fully functional in the older families, such as the *Hemerobiidæ*.

(4) By loss of the frenular bristles, reduction of the humeral lobe, and increase in the size of the jugal lobe, there arose the series of types seen in the Megaloptera, Trichoptera, and the true Jugate Lepidoptera (*Hepialidæ* and *Protothcoridæ*).

These parallel reductions must be conceived of as having taken place quite apart from one another phyletically, and probably at quite different geological periods. Though passing through the same series of reductions, these three groups arrive at quite different final results, as may be seen by comparing *Raphidia* (Text-fig.7) with *Oecetis* (Text-fig.9) and with *Charagia* (Text-fig.11).

(5) The highest specialisation of the old jugo-frenate type, still preserving the original characters of that type, is the jugo-frenate type of the *Micropterygidae*, in which the jugal lobe is folded under the forewing, so as to become directed forward and outward, and the frenulum becomes engaged in the groove so formed. Thus the jugal lobe functions as *the most archaic form of retinaculum yet discovered*.

(6) The origin of the specialised jugum of the *Hepialidae* and *Prototheoridae* is not to be traced directly from the Micropterygid type, but from an older, unspecialised, jugo-frenate type, such as we find in the Planipennia. The jugal lobe remains projecting outwards and downwards, not turned forwards to pass under the forewing. At first, it rested upon the costa of the hindwing, as in the older forms of Trichoptera. The frenulum, being useless, disappeared. A later and higher specialisation led to the lengthening and narrowing of the jugum, and finally to its adopting the position seen in most of the *Hepialidae*.

(7) From this, it follows that no existing type within the Lepidoptera of to-day represents the true ancestral form or Archetype of the Order. That Archetype must have possessed an *unspecialised, jugo-frenate coupling-apparatus*, probably without jugal bristles, as in the Planipennia to-day. The development of the specialised jugo-frenate type of the *Micropterygidae*, on the one hand, and of the specialised *jugate* type of the *Hepialidae* and *Prototheoridae* on the other, must have proceeded upon divergent lines.

(8) The frenate forms amongst the Lepidoptera are also derived from the archetypic jugo-frenate form, and not directly from the *Micropterygidae*, as is proved by the bristles of the frenulum maintaining their original direction. This line was

evolved simply by loss of the archaic jugal lobe, with correlated reduction in size and strength of the hindwing, as it became more and more dependent upon the fore in flight.

The most ancient type of frenate coupling is that preserved for us in the females of the whole series, where the bristles remain short and unspecialised, and the retinaculum is formed simply from the brush of stiff hairs or scales, that project forwards from the underside of the cubitus on the forewing.

In the males, there is a higher degree of specialisation, the frenular bristles becoming fused together and greatly lengthened, while a new and more effective retinaculum is developed from the underside of the radius in the forewing, in the form of a posteriorly projecting hasp or catch of chitin.

(9) The amplexiform types amongst the Lepidoptera Heteroneura are to be regarded as a series of separate developments (probably three in number) from originally frenate ancestral forms. Of these, the most evident connection would appear to be that uniting the frenate *Castniidae*, with their well developed humeral lobe and clubbed antennæ, with the very similar but non-frenate *Hesperiidae*.

(10) The only portion of the original coupling-apparatus left in the highly specialised Order Diptera is the jugal lobe, which becomes enlarged to form the *alula*.

We may now exhibit, in the form of a short Table, the state of the coupling-apparatus in the various existing groups, to which we must add the Archetypes of the several Orders, as these results will be required in the final discussion on the Phylogeny of the Orders. (See pp.316-317).

SUGGESTED CLASSIFICATION FOR THE LEPIDOPTERA.

The characters here studied, though not suitable for the main subdivision of the Order into two Suborders, may be legitimately used for the subdivision of the first of the two Suborders which we have based upon the wing-venation, viz., the Homoneura. They cannot, however, be used in subdividing the Heteroneura, since the three Amplexiform groups do not lie along one single line of descent.

We may, therefore, adopt the following classification:—

Order LEPIDOPTERA.

1. Suborder HOMONEURA.

Venation of fore- and hindwings closely similar and of primitive design.

Division A. JUGO-FRENATA.—With archaic jugo-frenate coupling-apparatus consisting of jugal lobe, humeral lobe, and frenulum; the jugal lobe turned under the forewing, and acting as a retinaculum for the forewing.....Family *Micropterygidae* (s.lat.).

Division B. JUGATA.—With specialised jugate coupling-apparatus; the frenulum absent, the jugal lobe elongated and narrowed, usually passing beneath the hindwing.....
.....Families *Hepialidae* and *Prototheoridae*.

2. Suborder HETERONEURA.

Venation of fore- and hindwings dissimilar, that of the hindwing being strongly reduced in comparison with that of the forewing. Coupling-apparatus of frenate type, except in three of the highest groups, in which the frenulum is absent and the coupling is of the amplexiform type.

(Division of the immense number of forms into superfamilies and families must be based upon wing-venational and other characters).

TABLE SHOWING THE CONDITION OF THE PARTS OF THE WING-COUPPLING APPARATUS IN THE VARIOUS ORDERS OF THE PANORPOID COMPLEX, INCLUDING THEIR ARCHETYPES.

Order.	Type (see below)	Parts of the Coupling-apparatus. (+ present, × vestigial, - absent).				Additions.
		Jugal lobe	Jugal bristles	Humeral lobe	Frenulum	
MEGOPTERA †:—						
{ Archetype ...	JF(a)	+	+	+	+	
{ <i>Choristida</i> & <i>Nannochoristida</i> ...	JF(a)	+	+	+	+	
{ <i>Mecoptida</i> ...	JF(t)	×	+	×	+	
{ Other families ...	JF(r)	×	×	×	×	
PLAUPENNIA:—						
{ Archetype ...	JF(b)	+	×	+	+	
{ Existing families ...	JF(b) or (r)	+	×	+	+	
MEGALOPTERA:—						
{ Archetype ...	JF(r)	+	—	+	×	
{ <i>Stalida</i> ...	JF(r)	×	—	—	—	
{ <i>Corydalida</i> ...	J(a)	+	—	—	—	
{ <i>Raphidiida</i> ...	JF(r)	+	—	×	—	amplexiform overfold. roughened tubercular area on forewing.

† Though the condition of the wing-coupling apparatus is not known for certain in the fossil Order Protomecoptera, we must conclude that its Archetype resembled that of the Mecoptera in this character.

TRICHOPTERA:—								
{ Archetype... ..	J(a)	+	-	-	-	-	-	amplexiform overfold. minute hooks along costa of hindwing.
{ Older existing types	J(a)	+	-	-	-	-	-	
{ Higher types	A M	or - -	-	-	-	-	-	
Diptera:—								
{ Archetype... ..	J(a)	+	-	-	-	-	-	
{ Existing families	J(d)	+	-	-	-	-	-	
LEPIDOPTERA:—								
{ Archetype	JF(b)	+	-	-	-	-	+	
{ HOMONEURA:—								
{ Jugo-frenata	JF(c)	+	-	-	-	-	+	
{ Jugata	J(s)	+	-	-	-	-	or ×	
{ HETERONEURA:—								
{ Frenata	F	-	-	-	-	-	+	retinaculum.
{ Amplexiformia	A	-	-	-	-	-	+	

In the second column of the above Table, the explanation of the abbreviations is as follows:—

- A = amplexiform type.
- F = frenate type.
- J = jugate type.
- (a) its archaic form.
- (d) with jugal lobe forming *abula*.
- (s) its specialised form, with jugal lobe forming a true jugum.

- JF = jugo-frenate type.
- (a) its archaic form.
- (b) the same with jugal bristles absent.
- (c) its specialised form, with jugal lobe turned under forewing, and direction of fremular bristles altered.
- (t) with parts reduced.
- (t) with jugal bristles fused to form a large tubercle.
- M = multihamulate type.

APPENDIX.

Note on the habits of flight and resting position of *Sabatinca*.

The following note, communicated to me in January last by Mr. A. Philpott, of Invercargill, N.Z., throws some new light upon the habits of this archaic genus:—"Since returning home, I have been watching for the new species of *Sabatinca* in a little bit of bush near my house. The weather is still broken, but on sunny days I have been able to learn a little about this species. I have seen several, always on or near certain mossy logs. The moth sits with its wings held roof-wise over the body. The head and thorax are held high up, as if ready to jump. When taking flight, the insect seems to spring into the air with closed wings, and then to fly forwards in a rather feeble and fluttering manner. They do not fly far; five or six feet is a rather long distance for them. The antennæ are always held widely separated, pointing obliquely forward and upward. I am keeping some in a jar with moss, in an endeavour to get some eggs and larvæ, but with no result so far. When touched, these captives spring an inch or two sideways, backwards, or forwards with equal ease. The feeble fluttering flight of this species, and I suppose it to be characteristic of the genus, is in marked contrast to the strong, dashing, swift motion of the *Hepialidæ*. The jugal lobe is folded back as in *S. incongruella*; the frenulum is similar to your drawing.

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EXPLANATION OF PLATES XXIX.-XXX.

Plate xxix.

- Fig.1.—Jugum of *Micropteryx aruncella* Scopoli, viewed from beneath ;
($\times 150$).
- Fig.2.—Frenulum of same, viewed from beneath; ($\times 125$).
- Fig.3.—Humeral lobe and bases of insertion of frenular bristles in *Sabatina incongruella* (Walker); ($\times 250$).
- Fig.4.—Frenulum of *Micropteryx thunbergella* Fabr.; ($\times 125$).

(Photomicrographs from descaled, cleared and mounted specimens. The jugal lobe in Fig.1, and the humeral lobes in Figs.2 and 4, have become cracked across near their bases, owing to the pressure of the cover-glass upon old and brittle material. Owing to the same cause, the frenular bristles have become pressed down upon the hindwing, and their correct directions somewhat altered).

Plate xxx.

- Fig.5.—Jugum of *Charugia eximia* Scott, viewed from beneath; ($\times 8$).
- Fig.6.—Frenulum and retinaculum of *Cephenodes janus janus* Miskin, ♀,
viewed from beneath; ($\times 5$).
- Fig.7.—Frenulum and retinaculum of *Hippotion scrofa* Boisd., ♀, viewed
from beneath; ($\times 7$).
- Fig.8.—Frenulum and retinaculum of *Hippotion scrofa* Boisd., ♂, viewed
from beneath; ($\times 6$).

(Photomicrographs from set specimens, not descaled. In Fig.7, the black bristles of the frenulum appear white, owing to the incidence of strong artificial light directly upon them).